SPONGE DISTRIBUTION AND LAKE CHEMISTRY IN NORTHERN WISCONSIN LAKES: MINNA JEWELL'S SURVEY REVISITED

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Minna Jewell conducted an extensive survey of the regional distribution of freshwater sponges in Northern Wisconsin, USA, during the 1930's, and examined factors that controlled the occurrence of sponges. We returned to 18 of her original 102 study lakes in 1996-97 to evaluate the long-term stability of the sponge distribution patterns that she reported. Comparisons of Jewell's data and our recent survey reveal a decline in the distribution of Spongilla lacustris in N. Wisconsin lakes during the past 60 years. Jewell had originally reported S. lacustris present in 10 of the 18 lakes that we re-visited. As of 1996, we were unable to find S. lacustris in 5 of these 10 lakes. In addition, we observed only I invasion by S. lacustris in a lake that previously had not contained this species. To test how effectively four chemical variables reported by Jewell (pH, colour, conductivity and SiO₂) could predict the distribution of S. lacustris, we applied a discriminant model to the historical data set. Based on these four variables, we found that discriminant models poorly predicted sponge distribution patterns in Jewell's original survey lakes and in 17 additional lakes surveyed in 1996. Our analyses indicate that S. lacustris can grow under a wide range of chemical conditions and suggest that other environmental variables are probably influencing sponge distribution in N Wisconsin lakes. \Box Porifera, ecology, freshwater sponges, fauna survey, Spongilla lacustris, Wisconsin.

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Freshwater sponges are present in many aquatic ecosystems and may comprise a major component of a lake's benthic community (Frost, 1991). Currently, 27 species of freshwater sponges have been identified in North America (Jewell, 1959; Penney & Racek, 1968; Harrison, 1974; Frost, 1991; Ricciardi & Reiswig, 1993). Most of these species have been reported from the N. United States and S. Canada, and regional distribution patterns indicate that biogeographic conditions may restrict the distribution of some sponge species (Penney, 1960; Penney & Racek, 1968; Jones & Rützler, 1975; Frost, 1991). At a more local scale, freshwater sponge distribution is influenced by environmental conditions within a particular lake or stream, however the relationship between the distribution of different sponge species and these environmental variables is not well understood.

In a classic and unusually detailed study for the times, Minna Jewell (1935, 1939) investigated the distribution of freshwater sponges in 102 lakes in the Northern Highland Lake District of Wisconsin, as a contribution to the comparative

limnological efforts of Birge, Juday, and their co-workers (Frey, 1963). Jewell identified 10 different sponge species and related their distribution to chemical variables in lakes. For each lake Jewell (1935, 1939) recorded dissolved oxygen, free- and bound- CO₂, pH, residue, SiO₂, conductivity, colour, and seechi depth. Results of her study indicated considerable variation in habitat requirements among sponge species and reported some level of correlation between abiotic environmental variables and species' distributions.

We revisited Jewell's efforts to examine the long-term stability of sponge distributions, and applied more modern analytical techniques to her original dataset. Of the ten sponge species reported by Jewell, *Spongilla lacustris* was by far the most prevalent. It occurred in 76 of the 102 lakes sampled, and was distributed throughout the entire range of abiotic conditions surveyed. Because of the widespread distribution of this species in Northern Wisconsin lakes (Jewell, 1935), we re-surveyed a subset of Jewell's original study lakes to determine if *S. lacustris* occurred in the TABLE 1. Distribution of *Spongilla lacustris* in 18 Northern Wisconsin lakes during Jewell's (1935) and 1996 surveys. Water chemistry data is presented for 1996 survey. Key: 0, sponges absent; +, sponges present; *,1996 findings were different from the 1935 dataset; ², Jewell referred to this lake as Muskelunge by Pickerel).

Lake	Survey 1935	Survey 1996	*	pН	colour (Pt, mg L ⁻¹)	Conductivity (µmho cm ⁻¹)	DRSi (µg L ⁻¹)
Anne	+	0	*	6.14	28.15	12	78
Bug	0	0		6.37	95.4	18	595
Crystal	0	0		6.57	6.04	12	14
Helmet	0	0		5.6	483.11	37	131
loyce	+	0	*	6.03	32,39	16	32
Little John Jr.	0	0		5.78	36.2	13	13
Little Pickerel	+	+		6.85	157.74	63	4409
Little Rock	+	+		6.4	19.89	11	65
Mann	0	+	*	9.44	45,6	123	2219
Mary	+	+		6.26	314.05	26	961
Muskelunge ²	0	0		7.55	114.11	80	7641
Nebish	+	+		7.04	23.03	18	147
Nixon	+	0	*	7.24	251.63	60	5973
Oswego	+	0	*	6.29	43.63	15	47
Street	0	0		6.00	23.91	15	47
Tamarack	+	+		7.34	129.04	73	889
U. Gresham	0	0		8.32	38.3	254	5191
Wishow	+	0	*	5.82	45.77	10	52

same habitats after 60 years, or if the distribution had shifted substantially. We focused our study on the relationship between S. lacustris and the lake chemical features, pH, colour, conductivity, and SiO₂, that Jewell (1935, 1939) suggested had the strongest apparent correlations with sponge distribution. Because Jewell's data were potentially limited by the analytical techniques available at that time, we applied modern statistical techniques to the original dataset to further test the degree to which a lake's chemistry could be related to sponge distribution. We applied discriminant analysis to her dataset, and used the resulting model to predict sponge distribution in a new set of 17 lakes surveyed during the summer of 1996. This provided a further test to determine how well chemical lake features are related to the occurrence of S. lacustris.

MATERIALS AND METHODS

Thirty five lakes in the Northern Highland Lake District of Wisconsin were surveyed for the presence of *S. lacustris* during the summer of 1996. Eighteen of these lakes were opportunistically selected from those in Jewell's (1935) survey. In addition, 17 new lakes were surveyed

to expand the original dataset. Our survey techniques included shoreline and littoral zone sampling by snorkeling and boating. A small jonboat, rake, and net were used to complement specimens collected by snorkeling. Water samples were collected in open-water regions of the lakes for chemical analysis. Small portions of sponges were brought back to the laboratory where they were air-dried and stored until spicule processing and identification following procedures described in Frost (1991). For each sample, dried sponge tissue was placed in centrifuge tubes and boiled in concentrated nitric acid for one hour. The remaining spicules were rinsed in ethanol, centrifuged, and slides were prepared for examination on a compound light microscope.

Water samples were collected in polyethylene bottles and processed in the laboratory. An Oakton WD-35607-10 conductivity meter

and an Accumet 900 pH meter were used for analyses. A spectrophotometer was used to determine water colour following procedures described in Cuthbert (1992). Dissolved reactive silica (DRSi) concentrations were determined colourimetrically by a Technicon Segmented Flow Auto Analyzer.

Discriminant analysis was used to examine the relationship between the distribution of *S. lacustris* and pH, SiO2, conductivity, and colour values reported by Jewell for the lakes she sampled in 1935. Our approach attempted to predict the presence or absence of *S. lacustris* in a study lake using an equation of the form:

$F = di_1 Z_1 + di_2 Z_2 + ... + di_n Z_n$,

where di is the weighted discriminant coefficient, Z is the discriminating chemical variable, and F is a categorical variable reflecting the presence or absence of a sponge (Digby & Kempton, 1994). The magnitude of the discriminant coefficient indicates the influence that the associated variable has on the distribution of *S. lacustris*. We applied discriminant analysis to the entire data set on the presence or absence of *S. lacustris* reported by Jewell for 102 lakes. We tested the efficacy of the discriminant analysis by a crossTABLE 2. Performance of discriminant model fit to 99 lakes from Jewell's (1935) survey. * = Jewell reported water chemistry data for 99 of the 102 lakes that she surveyed.

Spongilla lacustris	Jewell's (1935) Results	Discriminant Analysis Predicted Results
No. of lakes with sponges	73	50
No. of lakes without sponges	26	49
Total no. of lakes surveyed*	99	99

validation of the predicted results compared to the actual observed results reported by Jewell in all the lakes that she surveyed. In addition, the resulting model was applied to the 17 new lakes that we surveyed during the summer of 1996 to test whether this model predicted current distribution patterns accurately.

RESULTS

The distribution of *S. lacustris* was found to be the same as reported by Jewell in 12 of the 18 lakes re-surveyed. We detected *S. lacustris* present in one lake in which it had not been previously recorded (Table 1). Conversely, we did not find *S. lacustris* in 5 of the 10 lakes in which Jewell had reported its presence. However, we found no dramatic changes in lake chemistry to account for the disappearance of *S. lacustris* from these lakes.

Graphical analyses of the lake chemistry and sponge distribution reported by Jewell (1935), and the 35 lakes we surveyed in 1996, showed no obvious patterns between the pH, colour, conductivity, and DRSi values in relation to the presence or absence of *S. lacustris* (Fig. 1A-H). A comparison between our survey and that of Jewell (1935) revealed a general decline in the distribution of *S. lacustris* during the last 60 years (Fig. 1).

Our discriminant analysis of Jewell's dataset did not reveal any significant relationships between the pH, colour, conductivity, or SiO₂, and the presence or absence of *S. lacustris*, as reported by Jewell (Table 2). The discriminant analysis of Jewell's original data assigned discriminant coefficients to each chemical variable of 1.16 for pH, 0.46 for conductivity, 0.35 for colour, and 0.23 for DRSi. We cross-validated with Jewell's actual dataset to test the ability of these 4 coefficients to correctly predict the presence or absence of *S. lacustris*. We found no significant relationship between actual sponge distribution and the predicted distribution. Jewell had reported *S. lacustris* to be present in 73 of her study lakes and absent in 26. Using the original chemical values that Jewell reported as predictors, the cross-validation of her dataset predicted sponges to be present in 50 of the surveyed lakes and absent in 49, with an error rate of 49% (Table 2).

Our more recent survey also indicated that chemical variables are ineffective predictors of the occurrence of S. lacustris. We found S. lacustris in just over half (9 of 17) of the lakes that we included in our new survey (Table 3). Using the discriminant model derived from Jewell's data, and the chemical data from the new survey lakes, we had predicted that 13 of the 17 new survey lakes would contain S. lacustris, with an error rate of 49% (Table 4). Furthermore, the absence of any significant relationship between the occurrence of *S. lacustris* and the chemical gradients that we evaluated, as illustrated by the lack of any indication of correlation in Jewell's dataset or our recent survey, strongly indicates that some factors besides the chemical variables may dictate the presence or absence of S. lacustris.

DISCUSSION

The notion that tolerance to a wide range of abiotic factors is a major feature of the niche of some species, is a well-recognized phenomenon (Dunson & Travis, 1991). Our research emphasises the ability of S. lacustris to tolerate a wide range of chemical conditions, setting this species apart from several other groups of aquatic organisms. Abiotic factors have been shown to limit the distribution of several fish and zooplankton species, and to directly influence aquatic macrophyte community structure (Brown & Jewell, 1926; Rahel & Magnuson, 1983; Tilman, 1988; Webster et al., 1992; Arnott & Vanni, 1993). Our results do not indicate any significant relationship between the distribution of S. lacustris and lake chemistry. Recent surveys conducted in Norway and Connecticut also note the ability of S. lacustris to tolerate a wide range of abiotic conditions (Økland & Økland, 1996; De Santo & Fell, 1996). This tolerance may be a very important adaptation for the survival of this species in freshwater habitats and may account for its reported cosmopolitan distribution.

We most frequently found *S. lacustris* in small, sheltered regions of lakes, growing directly up from bottom sediments. In lakes with less suitable bottom substrate, smaller specimens were found

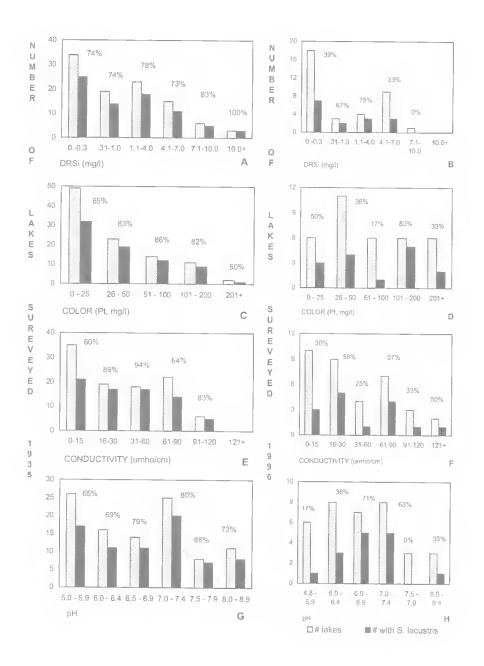


FIG. 1. Distribution of *S. lacustris* across chemical gradients for Jcwell's (1935) survey (A,C,E,G) and 1996 survey (B,D,F,H). Lighter bars indicate the number of lakes surveyed; darker bars represent the number of lakes containing *S. lacustris*. Note the overall decline in percentage of lakes with *S. lacustris* present. A-B, Dissolved reactive silica concentrations; C-D, colour; E-F, Conductivity; G-H, pH.

Lake	Survey 1996	pН	colour (Pt. mg L ⁻¹)	Conductivity (µmho cm ^{-r})	DRSi (µg L ⁻¹)
Aurora	+	6.86	190.67	93	6911
Benedict	+	5.99	48.37	8	136
Bittersweet	+	6.78	59.61	20	119
Crystal bog	0	5.1	98.71	8	158
Firefly	0	6.48	17.24	17	59
Fishtrap	0	7.7	40.27	93	4617
Frank	+	7.05	34.11	21	100
Goodyear spg	+	7.22	18.63	73	6390
Mystery	+	5.92	111.51	18	1348
Oherlin	+	6.68	27.48	15	153
Nixon creek	0	7.15	238.28	61	5712
Partridge	0	7.94	63.22	66	7015
Rainbow flwg	+	7.1	128.79	80	67
Round	0	8.61	85.96	106	4200
Sandy beach	+	6.87	239.17	34	3627
Tower	0	7.35	77.57	36	2845
Trout bog	0	4.76	202.67	17	60

TABLE 3. Distribution of *Spongilla lacustris* and water chemistry in 17 Northern Wisconsin lakes surveyed in 1996. These lakes were not included in Jcwell's (1935) survey. Key: 0, sponges absent; +, sponges present.

encrusted on the underside of logs, and on the woody roots of cranberry bushes (*Vaccinium* spp.). Tiny specimens were found growing in very low silica and conductivity habitats, most often on the tips of aquatic macrophytes, usually *Myriophyllum* and *Isoetes* species. *Spongilla lacustris* appeared well-adapted to a wide range of light conditions, and depending upon the colour of the water, was found anywhere from just below the surface in Little Pickerel Lake to depths of 3m in Littlc Rock Lake (Frost & Elias, 1990).

The trace amounts of DRSi found in some northern Wisconsin lakes do not appear to limit the occurrence of S. lacustris (Table 1). Observations of freshwater sponge morphology suggest, however, that DRSi plays an important role in the growth and skeletal strength of a sponge (Jewell, 1935; Kratz et al., 1991). Limited silica availability may result in decreased strength of the spicule skeleton, causing indirect negative effects on the distribution of sponges, perhaps by providing less protection against predation (Frost, Kratz & Elias, personal communication). Jewell (1935) recognised that DRSi was an important factor in determining the degree of skeletal development in S. lacustris, and consequently differentiated two different growth forms,

typical and atypical, correlated to the morphology of spicules. Jewell defined atypical specimens as those that had aberrant forms of spined microscleres from lakes with low silica concentrations. We also found several S. *lacustris* specimens from lakes with low silica concentrations to have finer, less robust spicules and smaller microscleres than those specimens from lakes with higher silica concentrations. For our analyses of Jewell's data we combined both the typical and atypical forms into one species classification.

Additional observations made during our field survey provided some insight into other environmental factors that may be influencing the distribution of *S. lacustris* in Northern Wisconsin lakes. We observed a slight decline in the presence of *S. lacustris* compared to its distribution in 1935. Many of the 12 lakes that we found no change in sponge distribution patterns are located in the Wisconsin State forest and have been protected from development for the past 60 years. Four of the five lales that are

60 years. Four of the five lakes that are now unoccupied by *S. lacustris* however (Anne, Joyce, Oswego and Wishow Lakes), have portions of their shorelines developed with privately owned cabins. Alteration of littoral habitats by development (e.g. removal of coarse woody debris; Christensen et al., 1996) may be negatively impacting the distribution of *S. lacustris* in these lakes.

Both our contemporary survey and that of Jcwell (1935) focused on the occurrence of *S. lacustris*, but not on it's biomass and prevalence, which varies substantially among habitats. It can be quite abundant in some situations (Frost et al., 1982; Frost & Elias, 1990), and nearly absent in others (Colby & Frost, personal observations). Also, while the overall distribution of *S. lacustris* may appear stable in some lakes, undocumented observations of significant yearly fluctuations

TABLE 4. Predictions of *Spongilla lacustris* distribution in 17 Northern Wisconsin lakes surveyed for the first time in 1996. The discriminant model used to make these predictions was parameterised using Jewell's (1935) dataset.

Spongilla lacustris	1996 Survey Results	Discriminant Analysis: Predicted Results
No. of lakes with sponges	9	13
No. of lakes without sponges	8	4
Total no. of lakes surveyed	17	17

have been observed previously (Frost, personal observation), but could not be quantified in either survey. The fact that we have not clearly linked species occurrence patterns with lake chemistry strongly suggests that other physical or biological factors are influencing sponge distribution. These factors could include associated vegetation, available substrate, predation, dispersion, climatic conditions and disease.

Apart from some interesting results reported by Jewell (1935) there is generally little information available on interactions between S. lacustris and its surrounding communities, including interactions with other freshwater sponge species. Competition and mutualism between different species of marine sponges has been relatively well documented (e.g. Rützler, 1970; Sarà, 1970; Wulff, 1997), and it is possible that these interactions occur in freshwater as well. Jewell reported nine other species that are not as common as *S. lacustris* in these lakes, and that we did not include in our survey. These other freshwater species may be more strongly influenced by lake chemical factors, and could also be influencing the distribution of S. lacustris. Recognition of freshwater sponges as active members of aquatic communities could lead to a better understanding of the relationships between freshwater sponges, environmental factors important to their survival, and their associated surrounding communities.

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AN OVERVIEW OF STROMATOPOROID DOMINATED MIDDLE DEVONIAN REEF COMPLEXES IN NORTH QUEENSLAND. Memoirs of the Queensland Museum 44: 99. 1999:-Middle Devonian stromatoporoid buildups are known from the Burdekin Subprovince and the Broken River Province in the Townsville hinterland, north Queensland.

Recent studies have placed these buildups within a reliable stratigraphic and sedimentologic framework. Buildups within the Burdekin Subprovince developed in a restricted near to proximal shore setting in a partially enclosed basinal setting. Those buildups within the Broken River province developed upon a more open marine shelf.

Major Burdekin stromatoporoid-coral buildups were of two types: low relief extensive biostromes and associated stromatoporoid pavements, and a biohermal system of one to two metres relief from the sea floor. Additional buildups of note are small patch reefs developed within nearshore siliciclastic muddy lagoons adjacent to granitic headlands. In a number of such metre scale buildups within dominantly siliciclastic settings, assemblages of stromatoporoids and corals show repetitive growth interruption surfaces suggesting episodic stress and killing events. Storm disturbance during development the biostromal pavements was high and an important sedimentologic factor for the 'reef' growth. Minor sponge s.s. buildups are known from the uppermost Burdekin Formation, but have not been studied.

In the Broken River Province, Givetian buildups are more extensive and can be traced on the hundreds of metrc scale, these have received little detailed sedimentologic study, but are of similar style to biostromal pavements from the neighbouring Burdekin Basin. Minor biohermal occurrences are found within the Papilio Mudstone, and formed on a muddy shelf, and include both stromatoporoid and sponge s.s. buildups.

Stromatoporoid taxonomy has revealed the presence of eight stromatoporoid communities in the Burdekin Basin, comprising 35 taxa. Dominant stromatoporoids were dendroids Amphipora, Stachyodes and Trupetostroma, frame building. Trupetostoma, Pseudotrupetostroma, Hermatostroma, Actinostroma and Ferestromatopora. Coenostroma, Clathrocoilona, and Stromatopora were accessory to reef growth. In the Broken River detailed taxonomic work has only been partially completed. Significant overlap exists at generic level with the two adjacent provinces, but species level differences are strong suggesting distinct partitioning of open marine versus embayment faunas. This phenomenon is reflected in other faunal elements (gastropods, rugose corals). \Box Porifera, stromatoporoid, biostromes,

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